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SOCIAL ORGANIZATION AND THE EVOLUTION OF CUMULATIVE TECHNOLOGY IN APES AND HOMININS

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Abstract

Culturally supported accumulation (or ratcheting) of technological complexity is widely seen as characterizing hominin technology relative to that of the extant great apes, and thus as representing a watershed in cultural evolution. To explain this divide, we modeled the process of cultural accumulation of technology, which we defined as adding new actions to existing ones to create new functional combinations, based on a model for great ape tool use. The model shows that intraspecific and interspecific variation in the presence of simple and cumulative technology among extant orangutans and chimpanzees is largely due to variation in sociability, and hence opportunities for social learning. The model also suggests that the adoption of extensive allomaternal care (cooperative breeding) in early Pleistocene *Homo*, which led to an increase in sociability and to teaching, and hence increased efficiency of social learning, was enough to facilitate technological ratcheting. Hence, socioecological changes, rather than advances in cognitive abilities, can account for the cumulative cultural changes seen until the origin of the Acheulean. The consequent increase in the reliance on technology could have served as the pacemaker for increased cognitive abilities. Our results also suggest that a more important watershed in cultural evolution was the rise of donated culture (technology or concepts), in which technology or concepts was transferred to naïve individuals, allowing them to skip many learning steps, and specialization arose, which allowed individuals to learn only a subset of the population's skills.

Key words: cumulative cultural evolution, ratcheting, hominin, great apes, sociability, mathematical model, innovation, imitation

Introduction

Recent studies have inferred the presence of culture, defined as multiple socially transmitted innovations, in chimpanzees and orangutans, based on geographic variation in behavior patterns or artifacts without obvious ecological or genetic correlates (Whiten et al., 1999; van Schaik et al., 2003a; Boesch, 2003; Kruetzen et al. 2011) and indirect indications of social learning in the field (Biro et al., 2003; Lonsdorf et al., 2004; Gruber et al., 2009, Jaeggi et al., 2010; Reader and Biro, 2010). These studies have allowed us to define more clearly what distinguishes human culture from that of the great apes, whose cultures probably closely resemble those of the last common ancestor of humans and the two chimpanzee species. Two major differences have emerged (Tomasello, 1999; van Schaik, 2004; Hill, 2009; Tennie et al., 2009): the cumulative nature of human technology, and the cumulative and normative nature of human cultural institutions. Our focus here is on explaining the origin of cumulative technology, which is widely considered to represent a watershed in cultural evolution.

The prevailing explanation is that cumulative technology is absent in great apes because they cannot imitate, and thus cannot reproduce novel actions with sufficient precision to serve as a uniform foundation for subsequent addition of accumulations. Thus, cumulative technology was thought to have arisen with Oldowan flake tools (Galef, 1992; Tomasello et al., 1993; Tomasello, 1994; Tomasello, 1999; Boyd and Richerson, 1996). We think this hypothesis is no longer supported, for two reasons. First, great apes in experiments can reliably transmit complex techniques, although the exact mechanisms remain debated, and second, they show some evidence of cumulative technology, if properly defined.

With respect to the imitation question, despite much recent work on nonhuman primates, no consensus on the mechanisms of observational social learning has emerged (Byrne and Tanner, 2006; Tennie et al., 2009; Whiten et al., 2009). Nonetheless, great apes have now been found to copy complex skills with sufficient reliability to maintain basic behavioral uniformity in two-target experiments in captivity despite the presence of alternative outcomes (reviews: Whiten et al., 2007; Whiten and Mesoudi, 2008; Dindo et al., 2011), which would suffice to maintain systematic differences in technology between nearby populations in the wild (Boesch, et al., 1994; van Schaik and Knott, 2001). Although some doubt remains (Tennie et al., 2006; Claidière and Sperber, 2010), most now agree that we should therefore look elsewhere than mechanisms of social learning to explain the elaboration of cumulative culture in humans (Price et al., 2009; Tomasello 2009).

To evaluate possible evidence for cumulative technology among great apes, we need a workable operational definition of cumulative technology, i.e. cumulative technological innovations that have been transmitted socially to the point of having reached high prevalence in a given population (habitual or customary status *sensu* Whiten et al., 1999). Cumulative innovations have been defined as those beyond what a naïve individual could invent during its lifetime (Galef, 1992; Tomasello, et al., 1993; Boyd and Richerson, 1996), i.e. outside its Zone of Latent Solutions (Tennie et al., 2009). However, this definition in effect assumes that the accumulation process has already proceeded to the point that it has become impossible for naïve individuals to invent the whole series of steps. It therefore excludes the initial steps of the accumulation process, i.e. those that may still be invented by an individual, which arguably are the very steps that historically determined the difference between cumulative and non-cumulative culture.

We therefore adopted an alternative approach. The build-up "implies the existence of superordinate representations abstracted from, and maintained over, the course of multiple subordinate events" (Stout, 2011), and is therefore usually accompanied by an increase in the size of the working memory, making the action series cognitively more challenging as it gets longer (Price et al., 2009). We accordingly defined the metric for the degree of accumulation (a.k.a. ratcheting) of a technique or learned skill as the number of distinct actions integrated as steps in a single functional sequence to reach an overall goal. One advantage of this metric is that this kind of complexity corresponds closely to that in terms of techno-units Oswalt (1976), which directly reflect properties of the tools themselves. It is in line with metrics developed for primate food processing (Byrne, 1995; Matsuzawa, 1996), and is also very similar to comparable metrics developed in archeology (Haidle, 2010; Stout, 2011), although we did not admit other criteria, such as the complexity of each individual action (which is also hard to define; Uomini, 2009) or the selectivity of the choice of raw material that is used to produce the tool. We excluded them because these aspects can be gradually improved over time through individual practice based on simple processes like associative learning, once the basic action has been put in place by ratcheting (e.g. Nonaka et al., 2010). It is important to stress that this system is preliminary and needs to be validated empirically through actual studies (for a recent attempt, see Sanz & Morgan, 2010). We will revisit this issue in the discussion.

The paradigmatic case of ratcheting is when an individual adds an existing technique used in a very different context or an entirely novel one to an existing one, and integrates them functionally. This can produce either a tool set (two or more tools used consecutively in a functionally integrated way), a composite tool (two existing tools combined directly), or a more complex tool (where subsequent actions modify an existing tool, adding functionality to it). Table 1 provides the definitions of the first ratcheting steps that can be recognized using this criterion, producing increasing technology levels (TL), and provides examples for both stick and stone tools.

Although cumulative technology defined this way is absent among orangutans, various examples have recently emerged for chimpanzees (Sanz et al., 2004; Sanz and Morgan, 2007; Sanz et al., 2009; Boesch et al., 2009). In the Goualougo triangle, for instance, the local chimpanzees use a tool set, consisting of a stout puncturing stick and a slender probe, to exploit subterranean termite nests. It is assumed that the probing tools were already well established, since they are found in many chimpanzee populations, before the stout puncturing stick was invented. Another example from the same site is the brush-tipped termite probe, where the regular termite probe (again assumed to be the starting point, given its common presence in other populations) undergoes an additional modification in which the tip is frayed, which makes it far more effective in gathering termites (which bite into the probe, and latch on more easily if the tip is frayed). This evidence from the wild is complemented by experimental work. Recently, Lehner et al. (2011) coaxed captive orangutans into making ratcheted innovations.

By these definitions, some chimpanzee technology in nature is cumulative, although the majority is not, whereas captive orangutans can be coaxed into making it. Thus, there is some overlap with the technology of the makers of the Oldowan (Table 1). Nonetheless, whereas all orangutan and most tools in the wild are TL1 and some chimpanzee tools are TL2 and perhaps even in one case TL3, regular Oldowan tools are TL2, but Oldowan tools used to modify wooden tools are TL3. Acheulean tools, in contrast, are TL3 or higher.

Given that great apes are now known to have sufficiently accurate powers of observational learning to allow ratcheting and that they show some evidence of cumulative technology in the wild or captivity, we need a new explanation of the major difference between humans and great apes in their technology. The goal of this paper is therefore to identify the factors responsible for cumulative cultural evolution of technology.

We begin by developing a model that correctly reproduces the known great ape patterns. Modeling cumulative technology is made easier by the presence of considerable variation among orangutans and chimpanzees, the two ape species showing extensive tool use in the wild. Most orangutan populations fail to show any systematic extractive tool use, but a few do and actually do so in multiple contexts (van Schaik et al., 2003a), and even show some variation within populations, depending on exposure to suitable role models (van Schaik et al., 2003b). All chimpanzee populations, in contrast, show at least some tool use (Sanz and Morgan, 2007), and some, as noted above, show evidence of ratcheting of technology. Having developed and tweaked the model for great apes, we then examine the hominin case by changing the model's parameter values in the direction of known or suspected changes during hominin evolution.

Methods

In this paper we propose a novel simulation model to explain the process of accumulation of technology. It is built using the same basic framework proposed by van Schaik & Pradhan (2003) to model tool use in great apes, which replicated geographic variation in orangutan tool use, and found it to be a function of variation in opportunities for social learning (see also Enquist et al., 2010). The current model simulates changes in a population's level of technology over time, as a result of individual opportunities for acquiring tool-use skills (either through invention or through social learning) at different levels of accumulation (TL0 through TL3). In the model, no skipping of technology levels is allowed; thus, for instance, TL2 is a prerequisite for reaching TL3, both in the innovation history and in ontogenetic acquisition. Even if this assumption does not strictly hold during ontogeny and some skipping is allowed, it remains likely that learning a skill is more difficult as TL increases.

We are interested in obtaining percentages of the total population engaged in various technology levels at every time-step given suitable ecological conditions. The model's parameters are listed and defined in Table 2, as are the best estimates of these parameters for great apes (see below for justification of the actual values used). We assume that every individual of the population has an intrinsic inventive ability (ε). The parameter α refers to the probability that an individual learns the skill socially from any of the nearest neighbors possessing higher TLs in a given year, subject to the constraint that in a given year it can only move up one TL at best. Social learning can take place because each individual in the population can be in tolerant proximity with some close neighbors. In the model, each individual is represented as a node in a regular graph with the degree 2κ (Harary, 1969; p 14), which is the number of close neighbors for each individual. In such a social network, all the nodes are arranged on a circle. Individuals can only learn from their nearest neighbors, i.e. the nodes to which they are directly connected. The value of κ is a function of the population's sociability, with high κ indicating high social tolerance. Note that we do not consider the effect of the number of demonstrators on skill acquisition through social learning. We chose this conservative rule because it is not known how the presence of multiple demonstrators adds up, and in the model most naïve individuals will often have only a single role model of a particular TL anyway.

The total number of nodes gives the size of the population (N). We could have modeled the population as a two-tiered system, with subgroups that internally show tight connections but are more loosely connected to other subgroups, but the effects would not be systematically different, except in the time it takes to reach particular TL values (see discussion).

For each combination of the parameters ε, α, and κ, we calculated the average fractions of the population that had attained the various technology levels after a suitably large number of time steps. We think of each time step as representing one year, which was also the time scale for the probabilities of innovation and acquisition through social learning. Each individual starts life at technology level 0 (TL0). It can then acquire higher technology levels through either personal innovation or social learning until it dies (implemented as reverting back to level 0). In each time step, the annual mortality rate (μ) sets the probability that the individual falls back to TL0 and age 0. Each individual has a window of active social learning (λ) that starts at birth and runs until this value is reached, representing the age at which it stops to learn socially, but after which it can still serve as role model. We also inserted a maximum age (M), although virtually no individual ever reached this. This structure produced a constant population that is roughly age-structured, but without having to introduce actual ages or other unrealistic simplifications.

As illustrated in the flow chart (Figure 1), the simulation goes through the following steps. We generate the social graph with degree 2κ. We then initialize the model at technology level 0 (TL0) for all individuals, who are initially all at age 0. In each time step (year), we sequentially check all nodes, and for each node, we check their survival. If the node survives and is within the age range in which it is capable of social learning, we check whether the node reaches the next TL through invention, and if not, whether it reaches the next TL through social learning. When all the nodes are traversed, we calculate the proportion of the population with TL0 through TL3 (or even higher TLs, see below). This procedure is then repeated for 10,000 steps, although equilibrium is almost always reached well before this time. To account for statistical variation in individual outcomes, the results reported in the following graphs are averages of 200 realizations of this procedure.

Parameter estimates for great apes

Because the model contains many parameters, high TL can be reached through many combinations. Thus, in order to increase the explanatory power of the simulations for hominins, we first determined the most realistic ranges for each parameter among great apes. We base these on the well-studied orangutan case of *Neesia* tool use (van Schaik and Knott, 2001; van Schaik, 2009), although we also examined the effect of each parameter over the whole range of values.

Starting with *N*, and given that orangutan populations do not consist of loosely connected subgroups, *N* is realistically in the range of hundreds or more, since most natural populations are in the range of up to a few thousand (Singleton et al., 2004). We kept values of α rather low (around 0.2). Great apes may be able to copy, but they are not good copiers (see above) and many activities are not performed long enough for much observational learning to occur, explaining why some profitable innovations originate but do not seem to spread (e.g. Yamamoto et al., 2008). In addition, many aspects of the techniques cannot be seen and must be acquired by individual practice, which is bound to take time (see also Stout, 2011 for humans). Finally, immatures take several years of observation alternated with practice to acquire tool-use techniques (Matsuzawa et al., 2001; Lonsdorf et al., 2004; van Schaik, 2004; E. Meulman, in prep.). Therefore, it is unlikely that α is much higher than 0.2 in ape populations for the more rarely invented skills whose origin and spread is modeled here. Obviously, for simpler skills, α levels could well be far higher, but here we are modeling the most complex technology shown by these animals in the wild. In a more conservative version of the model, one could reduce α levels, as TL increases, but this would not qualitatively change the outcome of the simulations (results not presented).

We put κ at low levels, since even in the most sociable orangutan populations, which have *Neesia* tool use, immatures do not associate with others than the mother more than about 60% of time, and although only weaned individuals are counted as associates, not all of these are fully adult (van Noordwijk et al., 2009). Since many associations are with a single independent individual only, there are about 2 nearest neighbors on average in these populations, giving $\kappa = 1$.

Given that we tried to replicate the distribution of *Neesia* tool use first, we decided that the innovation rate, ε, should be low, reflecting the absence of tool use in many populations inhabiting primary forests with *Neesia* trees, where it could potentially be seen (van Schaik, 2009). Since both seed extraction and nut cracking provide more calories than any other activity in these great ape populations (van Schaik and Knott, 2001), we must assume that individuals that invented this skill would keep on using it. By putting $\varepsilon = 0.0001$, we in effect assume that one in 500 individuals (given a mean annual mortality rate of 0.05, and thus an average lifespan of 20 years) will independently invent the technique, suggesting that in a large population of 500, one individual on average has come up with it. At $\varepsilon = 0.001$, this probability is still one in 50, so high that tool use should be seen in most orangutan populations with *Neesia* fruits. Since it is not, ε should realistically be in the order of 0.0001 or less.

Sumatran orangutans can live up to at least 50 years in the wild (Wich et al. 2004), so this was the maximum age (M) in the simulation. Annual mortality rates (μ) were set at 0.05, which may be somewhat high for orangutans (Wich et al., 2004), but is certainly at the low end for chimpanzees (Hill et al., 2001).

Orangutans do not effectively use tools until weaning age (roughly 7 years; van Schaik, 2004), and once adult may, like chimpanzees, gradually lose interest in learning in general, and social learning in particular (e.g. Tomasello et al., 1987; Matsuzawa et al. 2001; Tennie et al., 2010; Hobaiter and Byrne, 2010). Given that they may not be effective at learning complex techniques for the first year or two, this suggests that the social-learning window (λ) is in the order of 15 years or somewhat more. This is a rough estimate, because we do not have good estimates of how age affects social learning ability or interest.

Results

General model results

The model's output is the percentage of the population that has reached technology levels TL0, 1, 2, or 3, as a function of time (in years). In Figure 2.a, we plot this for a hypothetical great-ape population with moderate sociability ($N = 501$, $\alpha = 0.2$, $\kappa = 1$, $\varepsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$). At this level of sociability, TL1 can establish itself. In Figure 2.b, we have increased sociability to $\kappa = 2$. Now, TL1 establishes itself first, peaks, and then gives way to TL2, which in turn gives way to TL3. However, both TL1 and TL2 also stay around at low levels, reflecting the presence of individuals that have not yet reached the higher TL. This is therefore an example of a population in which ratcheted technology did evolve. We also examine the case where sociability is moderate ($\kappa = 1$), but innovation rate is two orders of magnitude higher than what we think is the case for the normal great ape situation ($\varepsilon = 0.01$). Figure 2.c shows that only a few members of the population reach TL3. Thus, the rate of innovation itself has far less influence on the TL reached by the average population member than the nature of the transmission conditions.

Great apes and cumulative technology

Orangutans and chimpanzees have similar cognitive abilities (Deaner et al., 2006; Herrmann et al., 2007; Tennie et al., 2010), and hence similar ε and α. They also have comparable life histories (Hill et al., 2001; Wich et al., 2004), and hence similar mortality rates (μ) and windows for social learning (λ), leaving only sociability (κ) and population size (N) to show enough geographic variation to affect variation in technology.

Figure 3 shows the results when the parameters were held constant at the values selected above (Fig. 2), but sociability, κ , corresponding to the number of possible tolerant experts in social learning, was varied. As expected, there is a strong effect of κ . The range from 0.5 (solitary, with mother as sole companion) to 2 (on average surrounded by 4 knowledgeable models, one of whom is the mother) correctly reconstructs the observed patterns among great apes (van Schaik et al., 2003a). In the most solitary situation ($\kappa = 0.5$), corresponding to the orangutans in most of Borneo, we see virtually no TL1, and nothing higher, even after many years (here, 10,000). The situation with $\kappa = 1$, corresponding to the social situation in orangutans inhabiting Suaq and other swamps on Sumatra's west coast but also many chimpanzee populations, leads to customary TL1, with the odd individual reaching TL2. Once κ reaches 2, we see that TL2 or even TL3 become customary, but it is not clear whether any known chimpanzee populations reach this level of sociability.

The degree of ratcheting that can be achieved by great apes is probably limited by the "affordance forcing" effect of the raw materials (see Table 1). This effect is expressed in the limited variability in great ape tools and the strict form-function correlation among these tools. These features reflect the biases in cognitive capacities of the species in question (the "latent solutions"), which evolved to detect and deal with the affordances of objects in the presence of suitable problems (Tennie et al. 2009). Affordance forcing limits the amount of accumulation that can be achieved with the same raw materials, justifying stopping the simulations at a moderate level, e.g. TL3; it is also the reason why in our model we do not consider distortions in techniques, which would have arisen due to error-prone copying. However, if we allow TL to increase, at $\kappa = 2$, in equilibrium a considerable proportion of the population had reached TL4, underlining the very strong effect of sociability on ratcheting. Thus, the main finding is that increased sociability will lead to ratcheting, and thus higher TL, among great ape populations.

The effect of *N*, in contrast, is entirely one of timing (Figure 4). At higher *N* the various TL levels are reached after a shorter number of generations, but the equilibrium levels are identical. Thus, in this model, *N* has no effect on the presence of the degree of accumulation of a particular technique, except in unusually small and isolated populations. This implies that a major demographic effect is expected only if populations frequently go extinct and areas are re-colonized by culturally naïve individuals, initially in small populations. Both the presence for over 4,000 years of nut cracking based on stone tools in chimpanzees (Mercader et al., 2002) and the unusually long temporal stability of orangutan populations in northern Sumatra (Nater et al., 2011) suggest that such demographic constraints were not ubiquitous. Moreover, known major habitat changes, such as recovery from the last glacial period, happened thousands, not hundreds, of years ago, long enough to produce equilibrium levels of cumulative technology. However, frequent local extinctions may have been an important factor in isolated populations or regions at the edge of the geographic distribution.

Hominin evolution until early Homo

Having successfully reconstructed the pattern of accumulation observed among great apes, we now examine whether the cultural changes in hominins with lithic technology could be a reflection of simple, immediate changes in socioecology. We do this by extending the standard great ape model as used above into parameter values known to characterize hominins. Morphological and archeological features suggest changes in sociability, social learning through teaching, and terrestriality.

The first evidence of routine butchering of large carcasses was around by 2.5 Ma (Semaw et al., 1997; de Heinzelin et al., 1999), in a way that suggests the presence of societies with unusually high sociability, needed to either acquire the prey through hunting or defend the carcasses against large carnivores (confrontational scavenging). This suggests a clear increase in κ, which is a reliable way to get a hominin population to reach higher TL levels (Figure 3). At $\kappa = 3$, we see that all adults reach TL3, well beyond what extant great apes can achieve. Allowing TL to move up freely yields a maximum at TL6, provided the affordances of the raw materials allow this.

There are many indications that extensive allomaternal care in the form of systematic food sharing or even provisioning, similar to what is seen among cooperatively breeding animals, began after the routine deployment of cooperative hunting subsequent to 2.5 Ma, and was firmly established by the appearance of *Homo erectus* around 1.7 Ma (Hrdy, 2009; van Schaik & Burkart, 2010; K. Isler and C. van Schaik, in review). Therefore, the demonstrators (already more numerous than earlier) probably also gradually began to engage in teaching, since teaching is common among cooperatively breeding animals with complex foraging techniques (Hoppitt et al., 2008; Rapaport and Brown, 2008; Burkart and van Schaik, 2010). Teaching, by definition, raises the social-learning ability, α. Figure 5 shows the effect of raising α, at two levels of sociability, κ. An increase of α beyond the level seen in great apes (for instance as a result of opportunitiy teaching, largely amounting to providing opportunities for appropriate practice: Caro and Hauser, 1992) provides a strong boost to technological accumulation. At higher levels of κ, this effect reaches a ceiling, when we keep TL fixed at 3. Nonetheless, in less than 1,000 years, such a population, despite having great-ape level cognitive abilities, will reach the maximum TL3 level. If we allow TL to evolve freely, a population with $\kappa = 3$ and $\alpha = 0.4$ will reach a maximum TL10, showing considerable ratcheting potential, probably well beyond what actually was possible with Oldowan techniques (see Table 1).

The processing of large animal carcasses necessarily took place on the ground. Among primates, systematic terrestriality can be shown to affect technological evolution because it leads to closer proximity (and thus higher κ) and systematic opportunities for affordance learning of the technology (and thus higher) (Meulman et al., in press). By the time *Homo erectus* appeared, these hominins had become systematically terrestrial (Bramble and Lieberman, 2004) and probably performed all skilled activities on the ground.

Discussion

Implications of the model

By ca 2.5 Ma, hominins already had reached lithic technology levels exceeding that of most chimpanzees (see Table 1), showing a definite advance toward cumulative technology. The simulations presented here suggest that this development in hominins was induced by changes in social organization that led to higher sociability, brought about by cooperative hunting or scavenging, followed by the adoption of full terrestriality and teaching elicited by systematic food sharing and provisioning, which further improved social transmission of skills. By the time *Homo erectus* appeared, some time before 1.7 Ma, the relevant social parameters (sociability κ , social learning ability α) had reached values that in the model guarantee stable cumulative technology.

The simulations imply that considerable technological accumulation can be achieved without any increase in innovation rate, population size, or development time (slower-paced life history). The fossil and archeological records also support this conclusion. First, the strong correlations between brain size and innovation ability in both birds and mammals (Lefebvre et al., 2004; Reader and Laland, 2002; Deaner et al., 2007) suggest that brain size can be taken as predictive of innovation level, ε . The Oldowan (Semaw et al., 1997) appeared well before major increases in brain size (Schoenemann, 2006). Indeed, our simulations show no effect of increased ε on the degree of accumulation of a particular technique (Figure 6, in which we assume $\alpha = 0.4$ and $\kappa = 2$), except that it speeds up the time at which maximum TL is reached (similar to the effect of *N*). Second, these hunting or scavenging hominins occupied higher levels in the trophic pyramid, and their population sizes are therefore likely to have been smaller than those of extant great apes. However, although higher population size or connectivity would have helped, they were not required: In smaller populations the same development (ratcheting of technology) would have reached the same equilibrium level, but would merely have taken longer. The time scale of changes observed in the archeological record indicates a very slow pace of change (Klein, 2009). Finally, the scant data on the life history of hominins predating *Homo erectus*, as deduced from tooth development (G. Schwartz, in prep.), indicate faster development than among extant great apes, and hence higher, rather than lower, mortality.

The model therefore strongly suggests that the first stages of cumulative technology required no increases in cognitive abilities (abilities to innovate or learn socially), because populations could achieve higher ratcheting levels so long as the essential innovations arose with some non-zero probability and were passed on with some non-zero probability. Obviously, these cultural changes were themselves likely to have served as the impetus for the subsequent evolution of greater cognitive abilities, especially via improved social-learning abilities, which secondarily improved innovative capacity as well (Wyles et a., 1983; van Schaik and Pradhan, 2003; Whiten and van Schaik, 2007; van Schaik and Burkart, 2011).

These results may appear to contradict the results of theoretical work on recent cultural accumulation in human evolution (Culotta, 2010), which stress the role of population expansion (Powell et al., 2009) and cognitive changes leading to increased innovation (Coolidge and Wynn, 2009). However, the pace of cultural change in (what is now visible in) the Oldowan and Acheulean was so slow that population size, which affects the time it takes for specific innovations to become established, hardly mattered. Moreover, increased innovation rate is both a direct and indirect outcome of accumulation itself. Thus, in the Middle and Upper Paleolithic, other processes may have determined cultural evolution.

The model's results also would suggest that considerable ratcheting of technology should have been possible, well beyond the Oldowan technology seen in the record for well over a million years, and should also still encompass the early Acheulean (cf. Table 1). This discrepancy may be more apparent than real because of the limitations of the archeological record, which does not retain any use of plant-based tools, alone or in combination with stone tools. Indeed, the greatest complexity would be reached for tool sets, functional sequences of (usually fairly simple) tools, as seen in the chimpanzees, but they likewise cannot be recognized in the archeological record. However, if the discrepancy is real, this implies that our model cannot be applied to later stages of hominin evolution. The most likely reason for this is that neither great apes nor early hominins could reach higher TL than the moderate levels (TL3 or TL4) examined in this model, due to limits on the amount of ratcheting imposed by the nature of the raw materials in combination with the cognitive biases (see above), or the increased cognitive difficulty of producing further modifications due to constraints on working memory.

Model assumptions

The model results obviously depend on our operationalization of ratcheting. First, it assumes, with Davidson and McGrew (2005) and Wynn et al. (2011), that the cognitive challenges posed by stick tools and stone tools both depend on the technology level (TL) and thus the depth of the planning hierarchy, despite clear differences in the kinds of actions performed on sticks and stones. Thus, a clear prediction is that the same population of a given species should reach similar TL in different kinds of technology.

Table 1 might seem to indicate that this assumption is wrong, as chimpanzees, the only great ape species to use any stone tools in the wild, do not reach higher TL in such tools, in stark contrast to stick tools, which have ratcheted up to TL3 in the wild. However, the discrepancy may only be apparent. Wild chimpanzees are doubly disadvantaged when it comes to ratcheting stone tools. Chimpanzees lack the need for artificial sharp edges (their teeth are long, strong and sharp enough for the problems they face, as pointed out by Davidson and McGrew (2005) as well as Toth and Schick (2009)), and even if they would discover the need for sharp tools, their environment largely lacks the suitable stone resources that could be knapped (Carvalho et al., 2008).

It is therefore important to explore the capacity of captive apes. As it happened, beside a pioneer study on one orangutan (Wright 1972) all work on great ape flaking focused on bonobos, not chimpanzees. Kanzi, the main tested bonobo developed, perfected, and later preferred, to throw the stones given to him against each other in order to produce blades. He developed this preference over the course of only 120 hours of experience (Schick et al. 1999). Importantly, Kanzi invented the throwing technique without having seen it modeled (thus, this is clearly a behavior within the bonobo ZLS) – and which is a behavior that remains to be analyzed in complexity and compared to two-handed flint knapping, in the way proposed by Bril et al. (2012). Certainly, the products thus produced were not fully comparable to Oldowan artifacts. Bril et al. take this to mean that Oldowan flint knapping included some more complex behaviors than we can find in modern great apes, but did not consider the possibility that Kanzi failed in this respect perhaps because he was biomechanically restricted (Toth and Schick, 2009) in a way that chimpanzees might not be. Moreover, a female bonobo called Panbanisha was observed “making stone tools, and she appeared to calculate angles before hitting the core” (Davidson & McGrew, 2005). It was also not the case that Kanzi could not flake in a hand-held, bimanual way. Kanzi may have simply realized that – for him – to flint knap in a two-handed way was less efficient than the throwing technique; perhaps not so much for cognitive, but perhaps merely for anatomical reasons.

Given the higher proficiency of tool use of chimpanzees in the wild in contrast to bonobos (e.g. Whiten et al., 1999), the best way to definitively test Bril et al.’s (2012) hypothesis is to test chimpanzees. At present, all we have is an unpublished study by Sarah Boysen and her team, who for the first time have provided chimpanzees with the need (a reward box with a rope-lock) as well as the necessary raw material to flint knap (a granite hammer stone and a raw flint rock). After two short demonstrations, one of the two tested chimpanzees flint knapped with high proficiency - at a level that, at preliminary analysis, clearly outperformed previously tested bonobos (S. Boysen, pers. communication, 12th July 2011). The resulting sharp edge was immediately used to cut through the rope that hindered the chimpanzee to get the reward. This to us shows the higher potential for flint knapping in chimpanzees in contrast to bonobos. Thus, the chimpanzee may not only have the cognitive capacity for Oldowan-like tools, it may also have the motor control to do so (somewhat in contrast, perhaps, to the case of bonobos), consistent with the critical assumption of our modeling study (cf. Wynn et al., 2011).

A second testable prediction of this operationalization of ratcheting is that developing individuals should make simpler versions of tools before they make the more ratcheted ones. This would seem to hold true of currently living great apes and extinct hominins. Thus, we predict that immature chimpanzees should learn to make termite probes first, and then later on learn how to fray the sticks’ ends to make them brushy, rather than to learn all of this at once (or if they do learn it all at once, they must learn it after longer practice, so probably at a later age than those in other populations that use simple probes). A third testable prediction is that ratcheted tools should have a more limited geographic distribution, and should often be nested inside the region of ‘ancestral’ simple forms from which they derive. Finally, it is to be hoped that neurobiological correlates of ratcheting can be revealed, which allow comparisons across species and tasks.

Future work should therefore test the model's assumptions. This may lead to modified conclusions. However, Sanz & Morgan's (2010) recent attempt to apply different systems of accounting for complexity to tools used by Goualougo chimpanzees revealed only modest discrepancies between them. Future work should thus also show to what extent classifications of complexity must also incorporate the choice of raw materials and the complexity of actions (Haidle, 2010; Stout, 2011).

Apart from the measurement of ratcheting, the model also assumed a role for sociability, the number of available role models. As an earlier model (van Schaik and Pradhan, 2003) predicted, evidence can indeed be found for enhanced culture in groups of great apes that are more sociable (Whiten and van Schaik, 2007). However, to the best of our knowledge the parameters identified here as the major ones for the accumulation of culture, have not yet been measured systematically in wild great ape populations and subsequently been correlated with the amount of ratcheting observed (let alone manipulated experimentally). This may also be due to the fact that accumulation is rare in great apes, and that thus any such correlation is hard to establish. We hope that future work in both field and captivity will test these various predictions.

Technological Evolution

The results of this study suggest a new perspective on the nature and timing of the major transitions in the cultural evolution of technology in primates and humans (Figure 7). The first phase began with the origin of simple culturally based technologies. It required the presence of extractive foraging and some cognitive abilities, enabling innovation and social learning (van Schaik et al., 1999). This level is reached by many great ape and some monkey (Ottoni and Izar, 2008; Gumert et al., 2009) populations, as well several non-primate lineages of mammals and birds (Whiten and van Schaik, 2007).

The second phase began with the origin of ratcheted technology. This can be elicited in captive apes and is found among some chimpanzee populations (and by inference early hominins), and is routinely present in late Pliocene and early Pleistocene hominins. We suggested here that this transition was made possible by increased sociability and terrestriality, and subsequently teaching (see also Tomasello 2009). However, this process probably also reaches some ceiling, set by material, cognitive (especially size of working memory), demographic and life-history limitations, reached by early *Homo.* The complexity of each particular technique may also reach a ceiling because an individual may have to learn various different techniques simultaneously, and thus cannot fully concentrate on any single technique. It may be difficult to break through this ceiling because each individual must learn to produce all the technology used in its society and is therefore constrained by learning time (although this gets longer as life-history pace slows down, and especially as the learning window expands). It is still possible, of course, that adaptations could have enabled hominins to move beyond this ceiling. For instance, lengthening the duration of the learning period (λ) will help. Nonetheless, some limitation should emerge, and our model strongly suggests that the prime mover was not cumulative culture per se.

Because of the constraints on learning time, we propose a third transition in cultural evolution to explain levels of accumulation beyond the ones we have modeled here. Moving beyond the results of our models, we speculate that it was caused by the appearance of donated technology, which relied on two major components: technology transfer and specialization (Figure 7). In technology transfer, naïve individuals would receive implements or concepts that they did not invent and could not design and produce themselves, allowing them to skip many steps in the ratcheting process and use these technologies to invent further ratcheted technologies. Thus, here we can begin to encounter cumulative culture in the sense of the appearance and subsequent routine use of innovations well beyond the innovative reach of individuals (cf. Galef, 1992; Tomasello, et al., 1993; Boyd and Richerson, 1996). Specialization, or advanced division of labor, means that individuals no longer need to learn all the technology used in a particular society, but can instead focus on acquiring a particular subset of skills. This almost inevitably produces higher technology levels in the population as well. Specialization can be recognized ethnographically by examining the TL level at which requests for help with the repair of tools and implements are made. One can also recognize it in the archeological record with the onset of long-distance trade (which presupposes specialization, unless the traded items were naturally occurring resources that were traded prior to processing them).

Both these novel features imply larger societies with a high level of cooperation and enough of a food surplus to support specialists that are not full-time food producers. Moreover, the high technology implies at least part-time sedentism and presumably trading of specialist products.

Because individuals can skip technology levels by using implements produced by other experts, and because different specialists acquire different skills, this third phase has a far greater potential to produce run-away cumulative technology. Hence, it is in this phase that demographic limitations (and therefore also time) become important, as stressed by recent archeological models that focus on relatively recent changes in the technology of *Homo sapiens* (Shennan, 2001; Henrich, 2004; Powell et al., 2009).

Conclusions

This modeling study showed that we could explain variation among orangutans and chimpanzees in the presence and degree of accumulation of their (mainly wood-based) technology with reference to varying sociability, which affects the opportunities for social learning. The degree of accumulation of technology well into levels shown by the most complex Oldowan tools can plausibly be attributed to further increases in sociability, and the introduction of teaching, which increases the probability of acquiring a skill through social learning. Thus, according to the model, no major cognitive changes, relative to extant great apes, were needed to explain the origin and initial elaboration of lithic technology in the hominin lineage, consistent with the observation that the two taxa had similar brain sizes. Our model also indicates that population (network) size is less important than previously thought – though it can be still important in timing, especially with regard to the rate of environmental change (d'Errico and Stringer, 2011). However, once populations consistently began to have highly ratcheted technology, selection may have begun to favor enhanced cognitive abilities, allowing faster developmental acquisition and (as a byproduct) the innovation of more complex techniques. Indeed, by the time the Acheulean appeared, hominin brain sizes exceeded those of extant great apes. This argument suggests that the seemingly autocatalytic increase in brain size during the early evolution of *Homo* was driven by technological evolution rather than by other factors such as social complexity per se.

Because considerable cumulative cultural evolution is possible with great-ape-sized brains, as implied by results form the wild and experiments in captivity, the ratcheted technology of hominins should no longer be considered qualitatively unique, although they subsequently pushed it to much higher levels than the extant great apes. We speculate that a truly qualitatively change in technological evolution came much later, in the form of donated technology, when individuals could use the products of others' efforts as their starting point, allowing them to skip many steps in the learning process, and individuals could also specialize in acquiring particular subsets of the skills present in the population as a whole.

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Figure captions

Figure 1: Flow chart showing the details of the simulation.

Final results are obtained by averaging over 200 such realizations.

Figure 2: Examples of scenarios in which technology at various levels evolved, showing the impact of sociability in comparison with the innovative ability in hypothetical great ape populations.

The plots show the equilibrium proportion of population using tools at technology levels 1 through 3 (TL1-3) as a function of time, assuming that TL3 is the highest attainable complexity of tools. (a) the parameter values representative of a hypothetical, typical great ape population ($N = 501$, $\alpha = 0.2$, $\kappa = 1$, $\varepsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions). Only TL1 can establish itself.

(b) If sociability is increased to $\kappa = 2$, keeping rest of the parameters same as in (a), the majority of the population is found to reach TL3.

(c) If the sociability is still at the typical great ape level, but innovative ability ε is increased by two orders of magnitude ($\varepsilon = 0.01$) compared to that in (a), only TL1 and TL2 are common, whereas only a small proportion reaches to TL3.

Figure 3: Variation in proportion of population using tools of varying complexity (TL1-3) as a function of sociability, κ. The error bars represent the standard deviation in the simulation outcomes.

The rest of the parameter values are as in Figure 2, viz., $N = 501$, $\alpha = 0.2$, $\varepsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions. For a fixed low social-learning ability, α, as κ varies from representative values for great apes to early humans, the major changes in the proportion of the population with tools at TL3 occur as κ increases from $\kappa = 1$ through $\kappa = 3$ (i.e. from 2 to 6 tolerant experts).

Figure 4: Proportion of the population using tools of varying complexity (TL1-3) as a function of time for varying population size.

Graphs show the proportion of the population using tools of technology level TL1 (a), TL2 (b), or TL3 (c), for various values of N assuming that TL3 is the highest attainable complexity of tools. The rest of the parameters are: $\alpha = 0.2$, $\kappa = 2$, $\varepsilon = 0.0001$,

$\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions. The total population size N affects only the time needed to reach equilibrium but not the equilibrium value.

Figure 5: Proportion of the population using TL3 tools as a function of social learning ability, α.

Two curves correspond to $\kappa = 1$ (solid curve; corresponds to low sociability) and $\kappa = 3$ (dotted curve; corresponds to higher sociability), respectively. The rest of the parameters are set to: $N = 501$, $\varepsilon = 0.0001$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions. An increase of $\alpha = 0.2$ to $\alpha = 0.3$ provides a strong boost to accumulation of technology, even at low κ (solid curve). Similarly high levels could be reached at even lower α values for higher sociability (dotted curve).

Figure 6: Proportion of the population using tools of varying complexity as a function of time for varying innovation rates: (a) TL1, (b) TL2, and (c) TL3.

The inventive ability, ε, is varied assuming that TL3 is the highest attainable complexity of tools. The rest of the parameters are: $\alpha = 0.4$ (higher than great ape level), $\kappa = 2$, $\mu = 0.05$, $\lambda = 15$; see Table 2 for definitions. Even orders of magnitude change in ε only affects the time needed to reach equilibrium but not the equilibrium value.

Figure 7: The culture pyramid (modified after Whiten and van Schaik, 2007), showing the hierarchical or nested-subset nature of various manifestations of culture.

Table 1.

Definitions and examples of technology levels. As one moves down in the table, technological accumulation increases. It is assumed that each level has reached high prevalence through cultural transmission. References are given only for cases not mentioned in the description of the model.

Techno-logy level	Description	Examples sticks	Examples stones
TL0	A single action (use object as tool)	Use a stick found nearby to poke into hole	Use a stone found nearby to pound nuts or bones[a]
TL1	A single action, followed by other coordinated action (use object as tool on prepared substrate)	Take a stout branch found elsewhere to a suitable anvil and use as a wooden hammer	Take a stone found elsewhere to a suitable anvil, and use to pound
TL1	A single action or set of closely related actions on one object, which is subsequently used as a tool *(tool manufacture)*	Break a twig from a branch, trim to size (and perhaps remove side-twigs, etc.), and use as tool	Hit stone on hard surface to produce flakes, through the anvil or throwing techniques[b], and use flakes as tool
TL2	Two distinct, subsequent actions on one object, which is subsequently used as tool *(composite tool)*	Prepare a twig to become a probe, and subsequently fray the end of the probe, thus improving its efficiency[c]	Not applicable due to body restrictions (body actions on stones are meaningless)
TL2	Integrated actions on two distinct objects, which are each produced separately (*tool set*)	Use of a separately prepared perforating stick to create a tunnel, followed by use of separately produced probe to extract termites[c]	Not applicable due to body restrictions
TL2	Co-action, two carefully integrated actions on two objects, one in each hand	Not applicable due to material restrictions (wood vs. stones)	Hitting a hand-held stone core with a stone hammer to produce an Oldowan flake (using hard-hammer percussion or bipolar technique) [b]
TL3	Use a made tool to modify another tool *(combining manufactured tools)*	Not applicable due to material restrictions	Use an Oldowan flake, produced earlier, to sharpen a stick for more effective use[e]
TL3	Use co-action (TL2) many times in a coordinated sequence	Not applicable due to material restrictions	Produce an Acheulean hand axe[b]

TL3	Use two different co-actions in integrated sequence	Not applicable due to material restrictions	Use hard hammer to prepare a core, followed by soft hammer, to produce flakes off an Acheulean handaxe[b]
TL3	Integrated actions on 3 distinct objects, which are each produced separately	Use of separately prepared pounding stick, followed by a lever tool, followed by a dip stick to obtain honey from bee nests[d]	Not applicable due to body restrictions
TL4	As in TL3 above, then add resharpening with different hammer	Not applicable due to material restrictions	As in TL3 above, followed by resharpening[b]

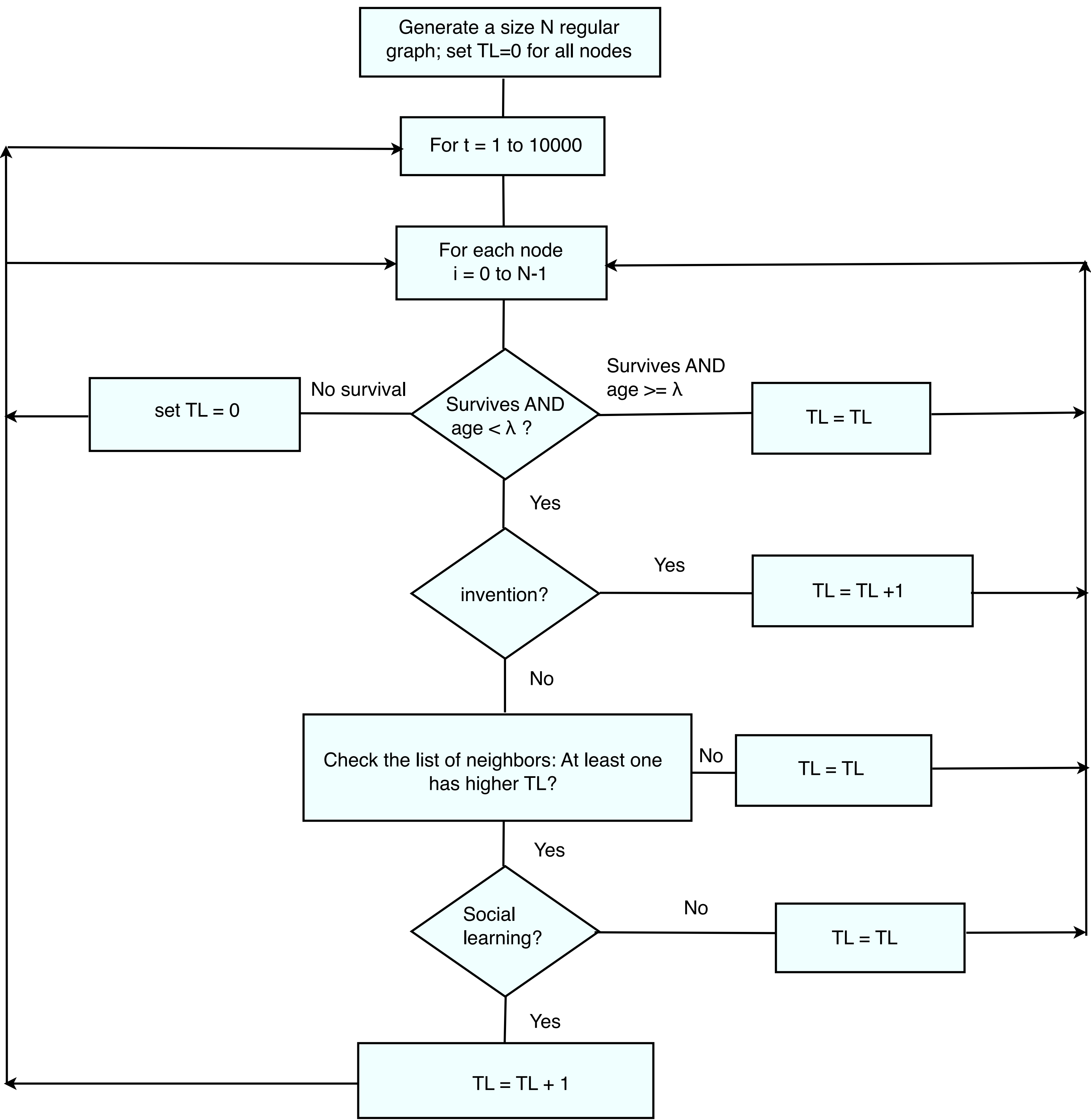
a- as in monkeys: Gumert et al., 2009; Ottoni and Izar, 2008; b- Schick and Toth, 1993; Boysen, personal communication; c- Sanz et al., 2009; d- Sanz and Morgan, 2007; e- Dominguez-Rodrigo et al., 2001.

Table 2.

Definition of the main parameters used in the model and the best estimates of the same for great apes (details of the estimates are provided in the SI).

Parameter	***Description***	***Best estimates for great apes (details in SI)***
$\varepsilon\,(0 \le \varepsilon \le 1)$	Inventive ability: Probability of acquiring a particular skill in one time step in the absence of social influence	0.0001 (i.e. approximately one in 500 individuals invents assuming annual mortality rate at 5%)
$\alpha\,(0 \le \alpha \le 1)$	Social learning ability: Probability of learning a particular skill in one time step under social influence from any of the skilled neighbors	0.2 (rather low value because great apes are not good copiers)
$\kappa\,(1 \le 2\kappa \le N)$	Sociability, or opportunities for social learning: Number of individuals in the social unit that are directly connected to the focal individual as possible experts from whom social learning is possible. The focal individual has 2| nearest neighbors to learn from. The parameter | is a constant for a given regular graph (the number of connected neighbors on one side of the individual).	1 (i.e. association with only two individuals most of the time: mother and another associate)
μ	Annual mortality: proportion dying each year	0.05 (average rate if orangutan and chimpanzee populations considered together)
λ	Age marking the end of active social learning ends	About 15 years
M	Maximum age reached in the wild	50 years
N	Population size	About 500

Figure 1



Generate a size N regular graph; set TL=0 for all nodes
For t = 1 to 10000
For each node i = 0 to N-1
No survival
set TL = 0
Survives AND age < λ ?
Survives AND age >= λ
TL = TL
Yes
invention?
Yes
TL = TL +1
No
Check the list of neighbors: At least one has higher TL?
No
TL = TL
Yes
Social learning?
No
TL = TL
Yes
TL = TL + 1

Figure 2

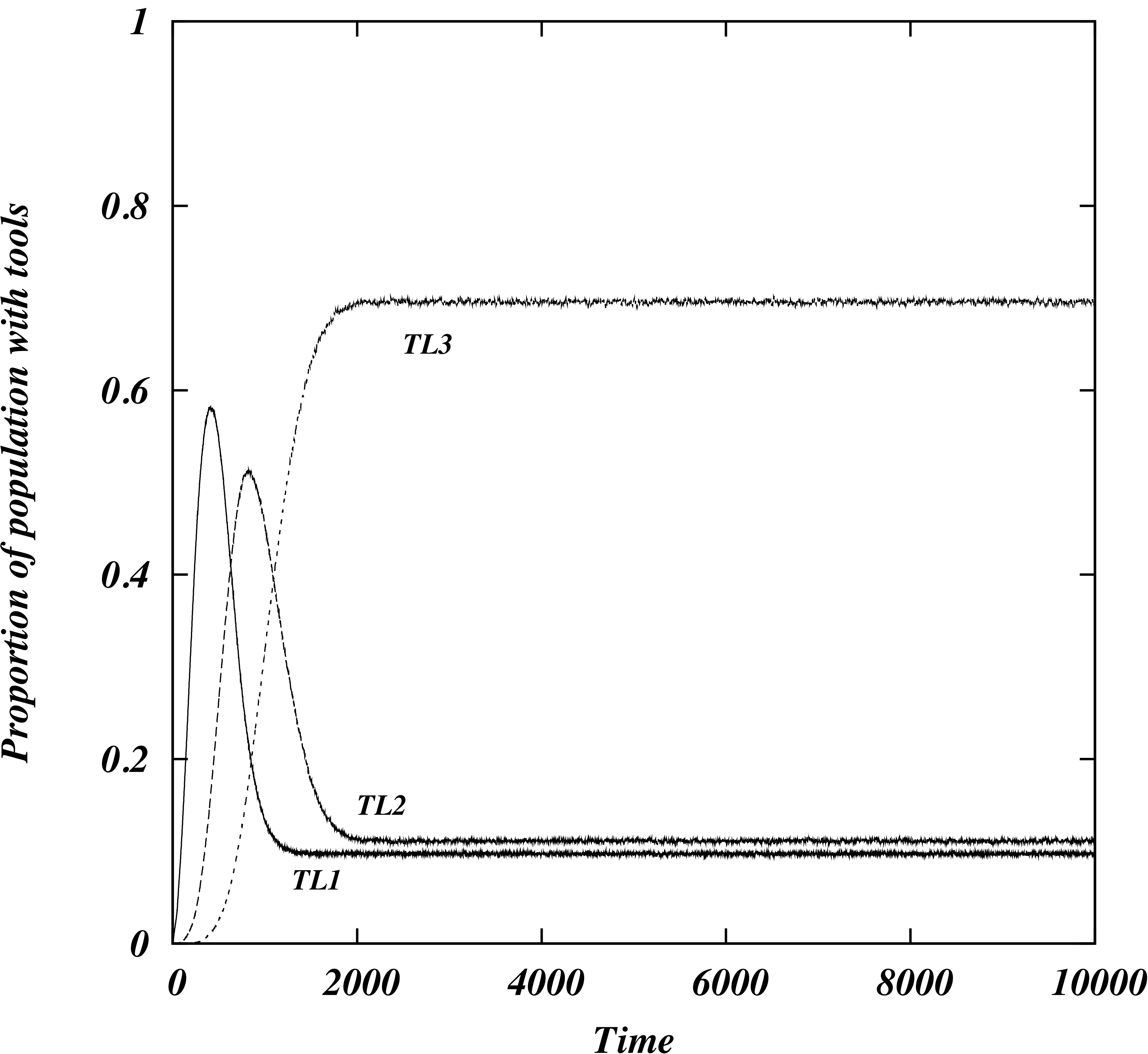
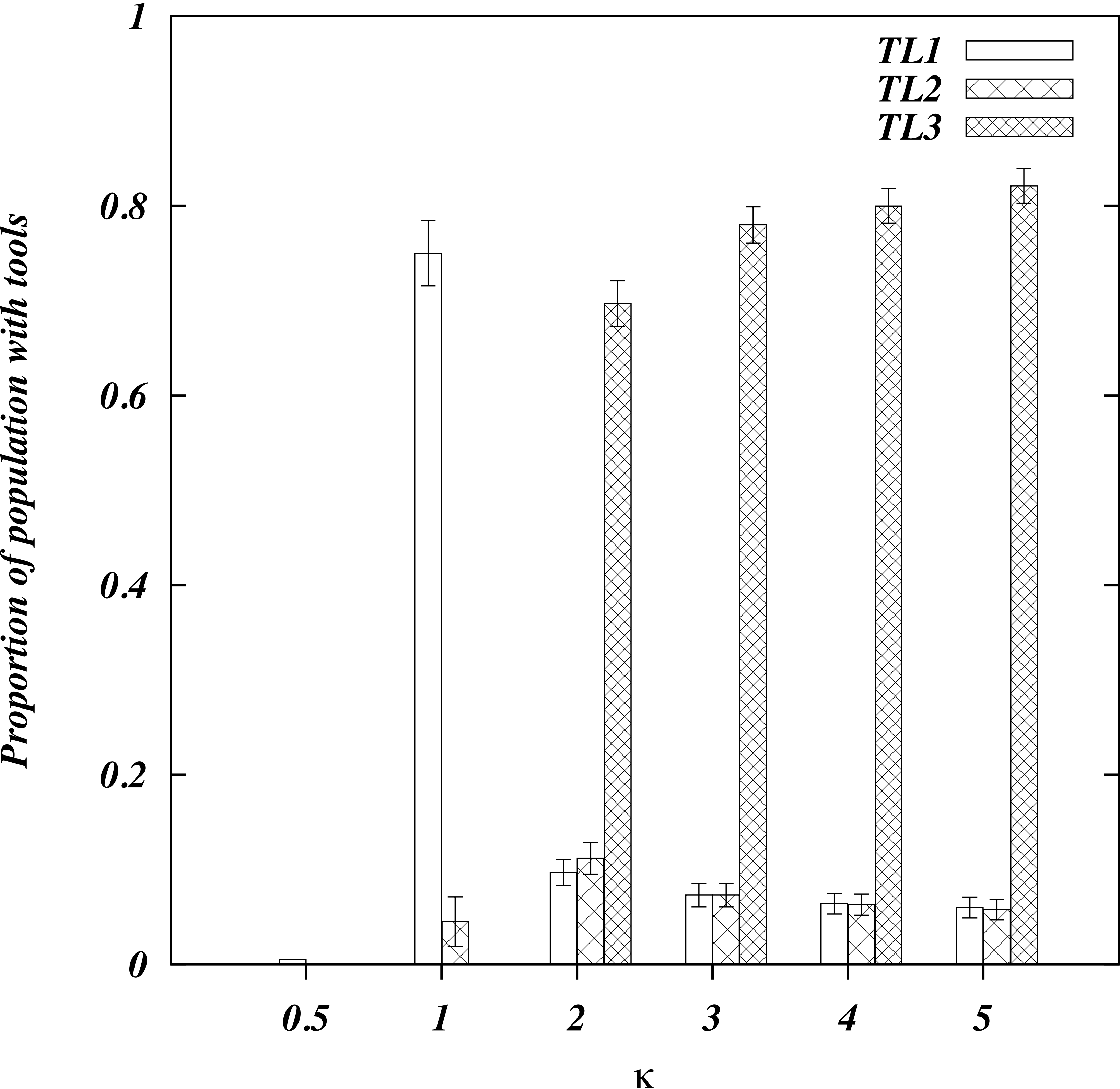

1
0.8
0.6
0.4
0.2
0
0
2000
4000
6000
8000
10000
Time
Proportion of population with tools
TL3
TL2
TL1

Figure 3



Proportion of population with tools
1
0.8
0.6
0.4
0.2
0
TL1
TL2
TL3
0.5
1
2
3
4
5
κ

Figure 4

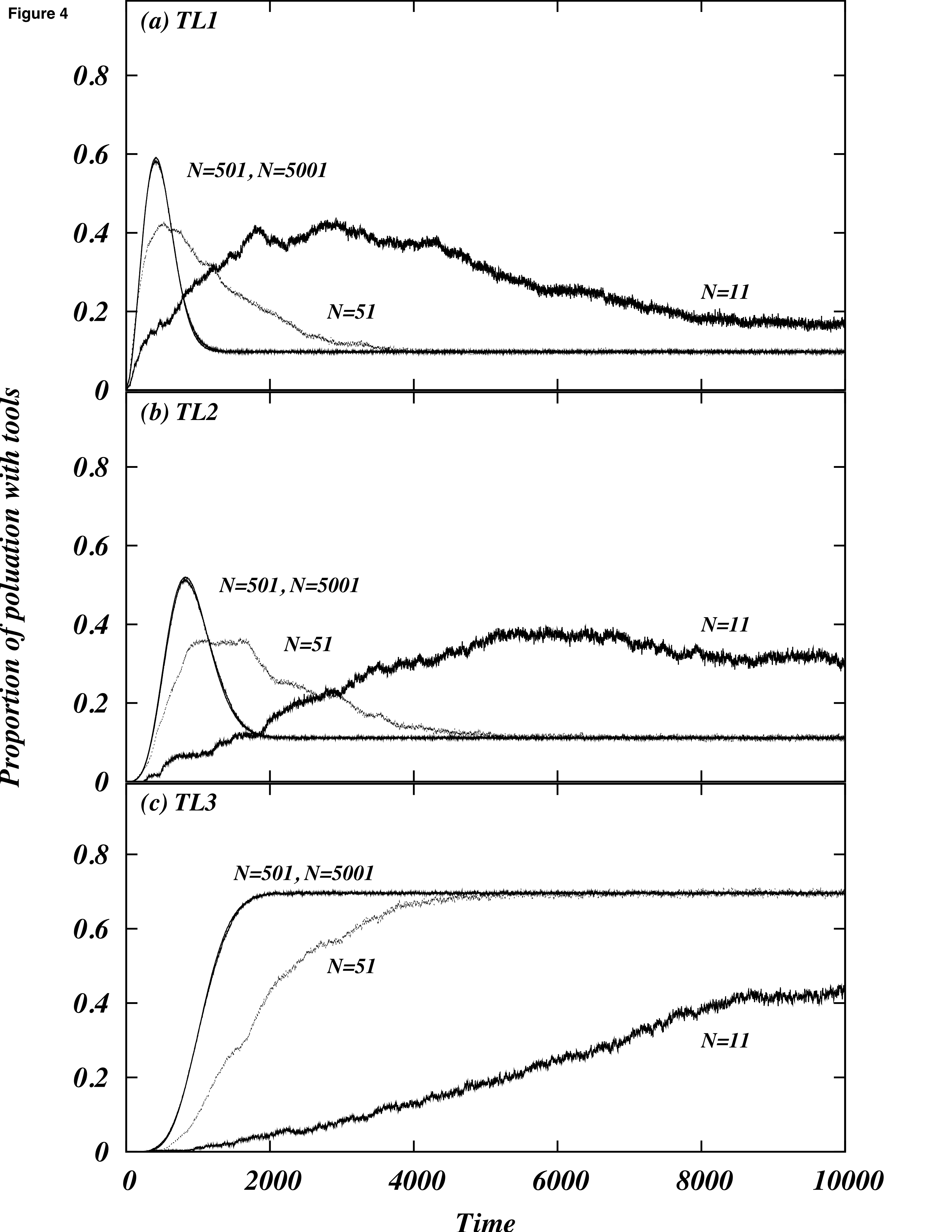

(a) TL1
N=501, N=5001
N=51
N=11
(b) TL2
N=501, N=5001
N=51
N=11
(c) TL3
N=501, N=5001
N=51
N=11
0
0.2
0.4
0.6
0.8
0
2000
4000
6000
8000
10000
Time
Proportion of poluation with tools

Figure 5

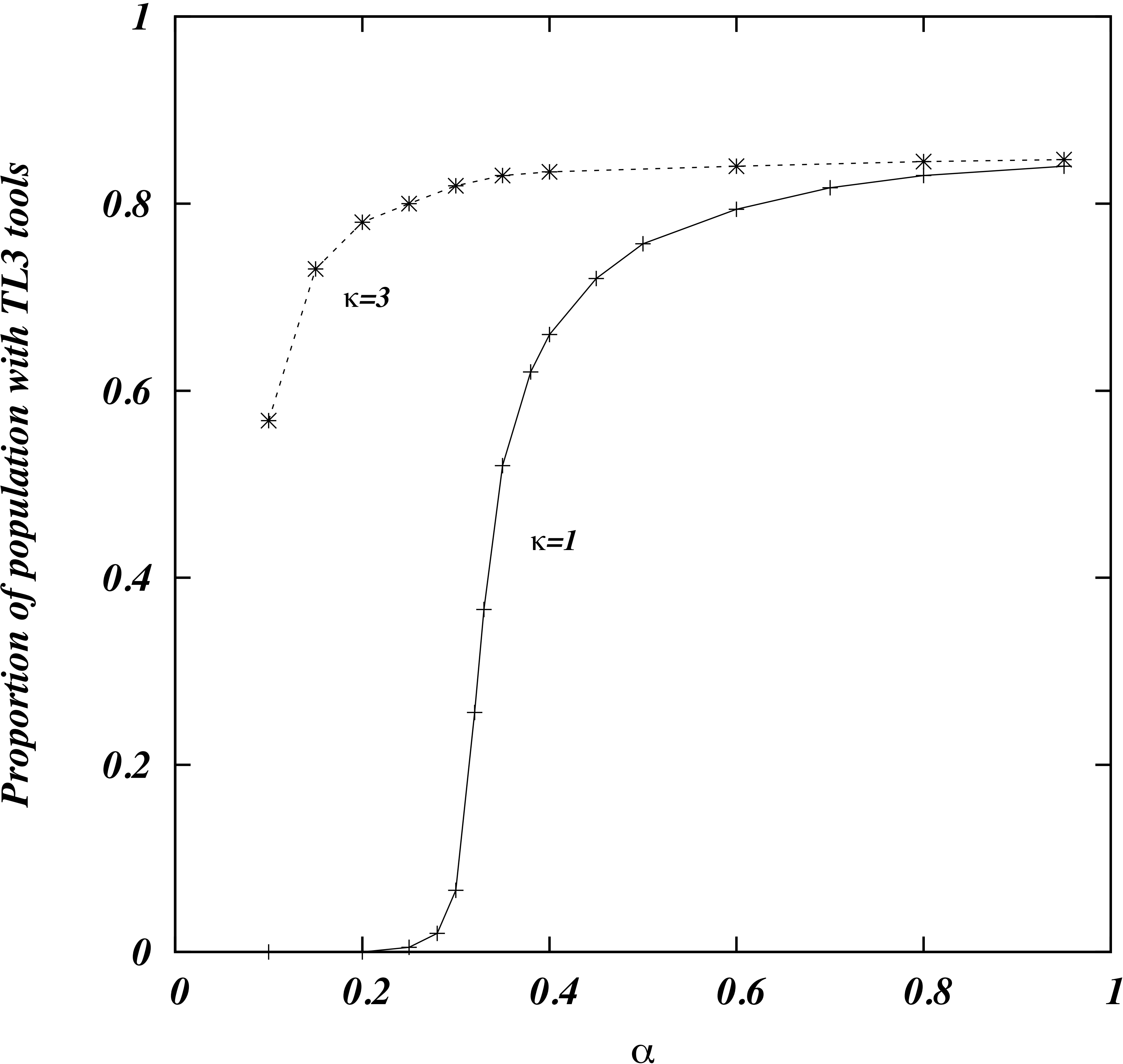


Figure 6

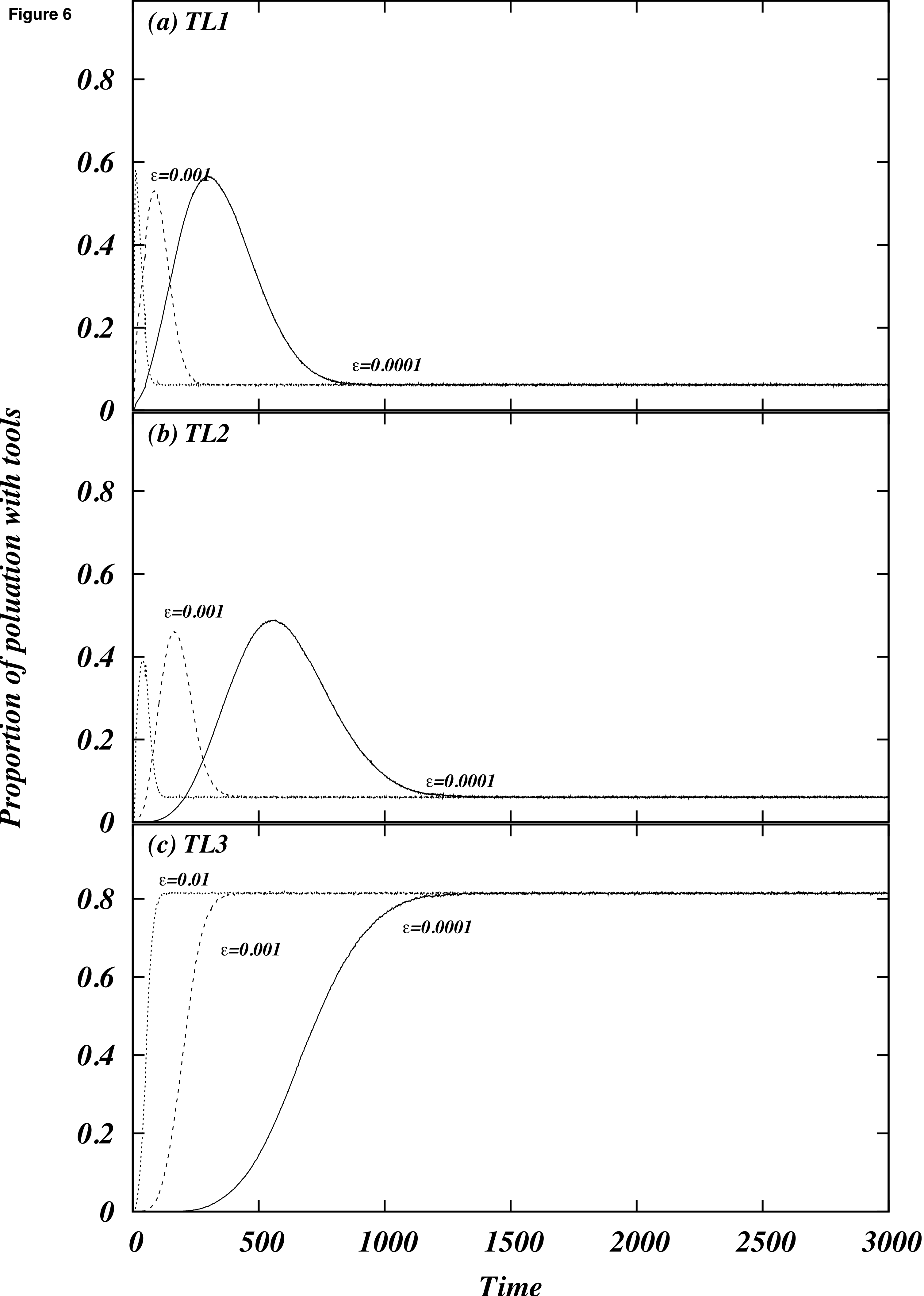

(a) TL1
ε=0.001
ε=0.0001
(b) TL2
ε=0.001
ε=0.0001
(c) TL3
ε=0.01
ε=0.001
ε=0.0001
0.8
0.6
0.4
0.2
0
0
500
1000
1500
2000
2500
3000
Proportion of poluation with tools
Time

Figure 7
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